Response of benthic fauna to experimental bottom fishing

Received: 25 August 2017 | Accepted: 20 February 2018

DOI: 10.1111/faf.12283

ORIGINAL ARTICLE

WILEY FISH and FISHERIES

Response of benthic fauna to experimental bottom fishing: A global meta-analysis

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Funding information
Glacier Fish Company LLC U.S.; Nippon Suisan (USA) Ltd.; American Seafoods Group U.S.; Pesca Chile, S.A.; Pacific Andes International Holdings Ltd.; Sanford Ltd. N.Z.; Sealord Group Ltd. N.Z.; South African Trawling Association and Trident Seafoods; UK Department of Environment, Food and Rural Affairs, Grant/Award Number: project MF1225; European Union (project BENTHIS EU-FP7 312088), Grant/Award Number: project BENTHIS EU-FP7 312088; US National Oceanic and Atmospheric Administration (RAM); The Food and Agriculture Organisation of the UN; Blumar Seafoods Denmark; Clearwater Seafoods; International Council for the Exploration of

Abstract

Bottom-contact fishing gears are globally the most widespread anthropogenic sources of direct disturbance to the seabed and associated biota. Managing these fishing disturbances requires quantification of gear impacts on biota and the rate of recovery following disturbance. We undertook a systematic review and meta-analysis of 122 experiments on the effects-of-bottom fishing to quantify the removal of benthos in the path of the fishing gear and to estimate rates of recovery following disturbance. A gear pass reduced benthic invertebrate abundance by 26% and species richness by 19%. The effect was strongly gear-specific, with gears that penetrate deeper into the sediment having a significantly larger impact than those that penetrate less. Sediment composition (% mud and presence of biogenic habitat) and the history of fishing disturbance prior to an experimental fishing event were also important predictors of depletion, with communities in areas that were not previously fished, predominantly muddy or biogenic habitats being more strongly affected by fishing. Sessile and low mobility biota with longer life-spans such as sponges, soft

the Sea (ICES) Science Fund; Espersen Group; Independent Fisheries Limited N.Z.; Gortons Inc.; San Arawa, S.A.; The Alaska Seafood Cooperative; The Walton Family Foundation; David and Lucile Packard Foundation; American Seafoods Group US; Glacier Fish Company LLC US; Nippon Suisan (USA), Inc.; Pacific Andes International Holdings, Ltd.; Natural Environment Research Council, UK, Grant/Award Number: NE/L003279/1; Marine Ecosystems Research Programme

corals and bivalves took much longer to recover after fishing (>3 year) than mobile biota with shorter life-spans such as polychaetes and malacostracans (<1 year). This meta-analysis provides insights into the dynamics of recovery. Our estimates of depletion along with estimates of recovery rates and large-scale, high-resolution maps of fishing frequency and habitat will support more rigorous assessment of the environmental impacts of bottom-contact gears, thus supporting better informed choices in trade-offs between environmental impacts and fish production.

KEYWORDS
dredging, effects of trawling, fishing impacts, invertebrate communities, systematic review, taxonomic analysis

1 | INTRODUCTION

Fisheries that use bottom-contact gears are the most widespread source of anthropogenic physical disturbance to global continental-shelf seabeds (Eigaard et al., 2017). Subtidal bottom fishing gears include otter trawls, widely used to target gadoids, flatfishes and prawns (Henry et al., 2006; Sanchez, Demestre, Ramon, & Kaiser, 2000), beam trawls used to target flatfishes on sandy bottoms (Kaiser et al., 1998; Rijnsdorp et al., 2008), towed dredges used to target scallops or other bivalve molluscs on sandy and gravelly bottoms (Carvalho, Constantinom, Pereira, Ben-Hamadou, & Gaspar, 2011; Hinz, Murray, Malcolm, & Kaiser, 2012) and hydraulic dredges used to target deep-burrowing bivalves (Hall & Harding, 1997; van den Heiligenberg, 1987). Intertidal gears include hand spades, used to dig up species such as polychaetes and bivalves (Dernie, Kaiser, & Warwick, 2003) and rakes, which are operated manually (e.g. hand rakes) or mechanically and used to extract species such as clams and cockles (Kaiser, Broad, & Hall, 2001; Mistri, Cason, Munari, & Rossi, 2009).

Bottom fishing can cause direct mortality of biota as well as physical changes in sediment composition, topographic complexity and sediment biogeochemistry, which in turn can have effects on seabed communities (Collie, Hermsen, Valentine, & Almeida, 2005; Mayer, Schick, Findlay, & Rice, 1991; O'Neill & Ivanović, 2016; Sciberras et al., 2016). In the short term (2 to 3 days), the carrion generated as a result of direct mortality of organisms on the seabed, and by discarding of by-catch, produces food subsidies for scavenging species (Kaiser & Hiddink, 2007; Ramsay, Kaiser, Moore, & Hughes, 1997) and can lead to an influx of scavengers in recently fished areas (Collie et al., 2017). Over the longer term, however, chronic bottom fishing disturbance can lead to a reduction in community production, changes in trophic structure and function due to decreases in faunal biomass, numbers and diversity, changes to the body size- and age-structure of benthic populations and a shift towards communities dominated by fauna with faster life histories (van Denderen et al., 2015; Duplisea, Jennings, Malcolm, Parker, & Sivyer, 2001; Hiddink et al., 2006; McConnaughey, Syrjala, & Dew, 2005).

The growing adoption of ecosystem-based fisheries management has catalysed demands for advice on the sustainable management of bottom-contact gears (Pikitch et al., 2004; Rice, 2014). Developing such advice requires knowledge of the distribution and types of bottom fishing activity, the habitats impacted, the impacts of the gears in use and the potential recovery of seabed biota (Pitcher et al., 2016a; Rice, 2005). Significant progress has been made with describing the footprint of bottom fishing activity in many fisheries (Eigaard et al., 2017) but substantial work is also needed to estimate the impact and recovery resulting from different gear and habitat combinations (Pitcher et al., 2016a). Several environmental risk assessments for the effects of fishing (ERAEF), such as the "likelihood-consequence" approach (Fletcher et al., 2002), the "susceptibility-resilience" approach (Stobutzki, Miller, & Brewer, 2001) and "expert judgement" (Eno et al., 2013; O'Boyle & Jamieson, 2006; Smith, Fulton, Hobday, Smith, & Shoulder, 2007) have relied on qualitative estimates of relative levels of susceptibility or potential risk, limiting their ability to assess the sustainability of fishing impacts. Spatial and quantitative environmental risk assessment approaches that are based on the differences in sensitivity of different seabed habitats, and the spatial distribution of habitats and fishing activity are alternative approaches, but have been less commonly implemented due to the paucity of sensitivity and habitat data (but see Hiddink et al., 2006; Pitcher et al., 2016a, 2016b).

The proliferation of experimental studies of bottom fishing impacts, in which an area of the seabed is experimentally fished with a defined bottom fishing gear and at a known fishing intensity (number of times the gear passes over the “impact” study area), has enabled us to conduct a robust meta-analysis of all available experimental studies of bottom-gear impacts and estimate the parameters needed for spatial and quantitative environmental risk assessments. Our objective for this meta-analysis is to estimate parameters for depletion (the fraction of biota removed by a single trawl pass) and recovery rates for different fishing gears, habitats and taxa, to provide information on the relative local impact of different fishing gear and habitats, and to support the development of quantitative approaches for environmental risk assessments of fishing impacts. Our study extends and adds to previous meta-analyses of bottom-gear impacts by Collie, Hall, Kaiser, and Poiner (2000) and Kaiser et al. (2006) because additional studies of gear impacts have been published because these and other studies were screened for inclusion in the meta-analysis with a systematic review protocol that avoided biases in selection because we increased taxonomic resolution and because our analytical methods were updated to suit the available data and to examine the effects of a wider range of covariates that may account for depletion and rates of recovery.

2 | METHODS

2.1 | Data sources and study inclusion criteria

Experimental bottom fishing studies published up to 2014 were selected following a published protocol (Hughes et al., 2014) for systematic review (Higgins & Green, 2008; Pullin & Stewart, 2006). Briefly, the process generated a list of studies that examined the effects of bottom fishing gear on benthic invertebrates (infauna and epifauna) in experimentally fished intertidal and subtidal areas. Multiple electronic databases and bibliographies were searched for publications, using a range of Boolean search terms specified in the protocol of Hughes et al. (2014).

Studies were retained if they provided data for infaunal or epifaunal meio- or macro-invertebrates for one or more of a number of

TABLE 1 Description of fishing gears examined in the meta-analysis

Gear type	Description	Penetration depth (mean ± *SE*) cm	Disturbed area per experimental plot (m^2)
Otter trawl (OT)	A type of trawl that has two rectangular “doors” or “otter boards” to keep the mouth of the funnel-shaped net open horizontally while the net is being towed. A vertical opening is maintained by weights on the bottom and floats on the top	2.44 ± 0.69	8,000–3,360,000; 120,000
Beam trawl (BT)	A trawl that is towed on the seabed where the net is held open by a wood or steel beam	2.72 ± 0.72	1,200–20,500,000; 63,750
Towed dredge (TD)	In general, towed dredges consist of a metal dredge rigged with teeth along the lower leading edge and a net bag or chain mail belly bag to collect the catch. TD include clam dredges targeting species such as *Spisula solida*, *Ensis siliqua* and *Donax truncatus*, scallop dredges targeting species such as *Pecten fumatus*, *P. maximus*, *Argopecten irradians* and *Aequipecten opercularis*, mussel dredge targeting *Mytilus edulis*, and rapido trawling targeting scallops and flatfish	5.47 ± 1.28	12–50,000; 1,225
Raking (R)	Includes manually operated hand rakes and tractor dredges that use a blade to skim the sediment surface to collect bivalves such as cockles. These were grouped together because they rake sediment	5.21 ± 2.10	1–1,125; 36
Digging (Dg)	Bait digging and bait dredging were grouped together as these activities directly remove sediment, creating pits or potholes	15.7 ± 5.63	1–100; 4
Hydraulic dredge (HD)	This category includes hydraulic dredges and suction dredges that use directed jets of water under pressure (i.e. mechanical pumping of water) into the sediment to dislodge clams (e.g. *Arctica islandica*, *Mercenaria mercenaria*, *Ensis* sp., *Tapes* spp., *Cerastoderma* sp.) that are then collected in a chain mesh bag as the dredge bar passes through the fluidized sediment. Also included in this category is clam kicking which uses propeller wash from boat engines to suspend bottom sediments and clams in shallow water.	16.11 ± 3.35	12–50,000; 1,225

The mean (±*SE*, cm) penetration depth (PD) in soft sediments is provided for each gear type. The area disturbed per experimental plot (range and median area, m^2) by each gear type in the studies examined.

biological metrics (number of individuals, biomass and species richness, defined here simply as the number of species observed) at the level of species, genera, families and/or communities. Data from the studies were included in the meta-analyses if the mean, sample size and a measure of variability (e.g. standard deviation, standard error, variance, 95% confidence interval) were presented for biological metrics inside and outside an experimentally fished area (i.e. control-impact study, CI), before and after an area was experimentally fished (i.e. before-after study, BA) or for both (i.e. BACI study). Whenever means, sample sizes or variability measures were not available in the paper, the corresponding author was contacted to provide these data and the study was included if these data were obtained. We included studies that used otter trawls (OT), beam trawls (BT), towed dredges (TD), hydraulic dredges (HD), digging (Dg) and raking (R), described in Table 1, to create the fishing disturbance.

Data from a total of 122 studies described in 62 publications met our inclusion criteria and were used in our analyses (SI1 Appendix, Table SI1.1). Data from a further 34 publications could not be used because no measure of variability was reported (SI1 Appendix, Table SI1.2). The number of studies exceeded the number of publications because multiple studies can be reported in a single paper. A paper was separated into several studies when it described experimental manipulations: (i) under different environmental conditions (e.g. depth, sediment type) and at different geographical locations, (ii) using different fishing gear to create the fishing disturbance and (iii) under different fishing intensity regimes (e.g. fished 4 times vs. fished 20 times).

2.2 | Response measure

The magnitude of response of fishing disturbance was calculated as ln(mean in the impacted area/mean in the control area) or ln(mean after/mean before disturbance), and is hereafter referred to as the log response ratio, ln(RR) (Hedges, Gurevitch, & Curtis, 1999). Mean values were for number of individuals, biomass and species richness data. The log response ratio quantifies the proportional change that results from the disturbance and is appropriate given that the absolute number of individuals, biomass and species richness of taxa varied widely among studies (Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten, 1999; Hedges et al., 1999). Since different intensities of fishing in the experimental areas were used in different studies, the ln(RR) was adjusted to account for frequency of fishing in the experimental area (Equation 1), where f is the number of times a unit area was fished (e.g. at f = 1 the whole experimental area was covered once by the fishing gear):

$$\text{adjusted } \ln(\mathrm{RR}) = \ln(\mathrm{RR}^{\frac{1}{f}}) \tag{1}$$

Hereafter, reported values of ln(RR) have been adjusted. Negative values of ln(RR) indicate lower values of number of individuals, biomass or species richness in fished areas (impacted) relative to non-fished (control) areas. Positive values indicate higher values after fishing and are not expected except when the response measure is calculated for scavenging species. The back-transform of ln(RR) is readily interpretable as a proportional or percentage change. As is general practice in meta-analysis, the response ratios were weighted by the inverse of study variance, calculated from the mean ($\bar{X}$), standard deviation (SD) and sample size (n) values for each study, as shown in (Equation 2) (Borenstein, Hedges, Higgins, & Rothsein, 2009):

$$V_{\ln(\mathrm{RR})} = \frac{SD^2_{\mathrm{Impact}}}{n_{\mathrm{Impact}}(\bar{X}_{\mathrm{Impact}})^2} + \frac{SD^2_{\mathrm{Control}}}{n_{\mathrm{Control}}(\bar{X}_{\mathrm{Control}})^2} \tag{2}$$

This weighting procedure reduces the influence of studies with high within-study variability or small sample size relative to those with lower variability or larger sample size and therefore considered to be more reliable. The calculations of the response ratio and variance for BACI studies required small modifications to Equations 1 and 2 as detailed in SI2 Appendix, Text SI2.1.

2.3 | Resolution of analyses

Analyses of depletion and recovery were conducted for entire benthic communities as well as taxonomic groups. For communities, analyses used ln(RR) and $V_{\ln(\mathrm{RR})}$ calculated for the reported whole-community biomass, number of individuals and species richness and includes studies of infaunal and epifaunal meio- and macrofauna. For taxonomic groups, analyses used ln(RR) and $V_{\ln(\mathrm{RR})}$ calculated from number of individuals or biomass data aggregated to Phylum and Class level. In this case, mean and variance (i.e. standard deviation^2) of number and biomass data were summed across all species within each taxon and study, prior to calculation of ln(RR) and $V_{\ln(\mathrm{RR})}$.

The relatively low number of studies reporting biomass data (33%, N = 45 studies) precluded analyses of many combinations of gear and habitat effects. Therefore, rather than excluding biomass data from the analyses, response measures (ln(RR) calculated for number of individuals and biomass (together referred to abundance) were pooled in one analysis, on the basis that estimates of response for numbers and for numbers and biomass combined were very similar (SI3 Appendix, Figure SI3.1).

Carrion generated in fished areas has been shown to attract scavenging and predatory epifaunal species such as decapods, asteroids and ophiuroids within the first 48 hr following the disturbance (Kaiser & Spencer, 1996; Ramsay et al., 1997). Such short-term movements of mobile species in response to disturbance may mask the extent of reduction in the numbers or biomass of resident fauna in response to fishing at the experimental site. For the taxonomic group analysis, scavengers could be identified based on knowledge of the feeding behaviour of the species studied (SI4 Appendix, Table SI4.1). Data for these scavenging species collected within 2 days of experimental fishing disturbance were removed from the data-set prior to the meta-analyses. For the community studies, which did not report the abundance of individual species or taxa, it was not possible to exclude scavenging species directly. In these cases, epifaunal studies reporting data collected in the first two days following experimental fishing were removed (SI1 Appendix, Table SI1.1).

2.4 | Meta-analyses

Separate meta-analyses were carried out for community data and for taxonomic group data. The analyses were structured to assess the overall effect of bottom fishing (all gears and habitats combined), the effects of gear type and habitat type on initial response and recovery of benthic community, and different taxonomic groups. We also examine the effect of several other potential explanatory variables that may influence recolonization rates by adults and larvae and growth rates of individuals and populations following a disturbance event for community data, but not for taxon data as the number of replicates was not sufficient for such analysis. Our decision for examining gear type, habitat type and interaction effects separate from other explanatory variables is rooted in the trade-off between the number of covariates and the number of observations, as an overfitted model leads to poor estimation of regression coefficients, *p* values and R^2 values.

2.4.1 | Overall effect of bottom fishing

We used a weighted linear mixed-effects model (rma.uni function in R package metafor, Viechtbauer, 2010) with restricted maximum-likelihood (REML) estimator, to investigate the initial response and recovery of benthic invertebrates after fishing. Although post-impact recovery is likely to be non-linear (e.g. logistic recovery), such curves proved difficult to fit to the available data given the relatively low number of replicate studies. Hence, it was more practical to fit log-linear models to estimate recovery. The model examining the effect of fishing on benthic community was specified as ln(RR) ~ intercept + $\log_2(t + 1)$, where the intercept specifies the initial response caused by a trawl pass (i.e. ln(RR) at time = 0) and the slope indicates the rate of recovery. The aggregate response of species at Phylum and Class level to fishing was estimated from the model ln(RR) ~ $\log_2(t + 1)$ × Taxon, where *Taxon* was either Phylum or Class.

For reporting and ease of interpretation intercept values, which indicate the initial response to a trawl pass and are on the ln(RR) scale, were converted to response (%) = $(\exp^{\text{intercept}} - 1) \times 100$. Depletion is defined as a negative response. As an illustration, an intercept value of −1 represents a response of −63%, 0 represents no response and +0.7 represents a response of 100% increase. The time it takes for abundance or species richness in a fished area to return to the control value (i.e. recovery time, t_c) was calculated from estimated values of slope and intercept as the time at which ln(RR) is predicted to return to 0. Hereafter, this reporting terminology is adopted for all analyses. Because no studies reported on recovery beyond 3 years, we are reporting projected recovery times beyond 3 years as 3+ years. The Q_M statistic tests for differences among levels of the explanatory variables, gear type and habitat type. R^2 provides the amount of variability (in per cent) explained by the explanatory variable.

2.4.2 | Effects of gear and habitat type

Previous studies of bottom fishing impacts (Collie et al., 2000; Hiddink et al., 2017; Kaiser et al., 2006) provide evidence for increased impact when gears penetrate further into the sediment and faster recovery in coarse sediment (e.g. sand) than in fine sediment (e.g. mud), where natural disturbance from tidal currents and waves is generally low. Gear-specific and habitat-specific changes in initial response and recovery were therefore examined using *Gear* and *Habitat* as additional model variables. Six gear types were examined; otter trawls (OT), beam trawls (BT), towed dredges (TD), hydraulic dredges (HD), digging (Dg) and raking (R) (Table 1). Four sedimentary habitat types were defined: "gravel" if the percentage composition of gravel was more than 30%; otherwise, "mud" if the percentage of mud was higher than that of sand and "sand" if the percentage of sand was higher than mud. The percentage of sand or mud was greater than or equal to 60% in 98% of studies (120 studies out of a total of 122 studies). There were only two studies where sand was 54.75% and assigned as sand, and in the other study mud was 54% and assigned as mud. A fourth category, "biogenic" (which technically is a habitat rather than a sediment description), was used for studies on oyster reefs, *Modiolus* beds and seagrass meadows. This simple sediment classification was adopted for necessity; while the sediment descriptions and particle-size ranges extracted allowed a more highly resolved classification of sediment type to Folk categories (Folk, 1974), there were insufficient replicate studies within categories to run the subsequent analyses at this higher level of resolution.

We compared models containing main effect terms and interaction terms that addressed specific and ecologically relevant hypotheses for responses to fishing (see description and justification in SI5 Appendix, Text SI5.1). For example, ln(RR) ~ gear + $\log_2(t + 1)$: habitat examines the effect of gear type on the magnitude of initial response and of habitat type on the rate of recovery. We could not explore all gear and habitat interactions because the range of gears that can be used will depend on habitat type (e.g. towed dredges are used mostly on sand, digging does not occur on gravel). The numbers of studies by habitat and gear type, for each biological metric (abundance, species richness), are given in SI6 Appendix, and were regarded insufficient for analysis if the number of replicate studies was less than 3.

Gear-specific and habitat-specific effects on different taxonomic groups were examined separately for bivalves, gastropods, echinoderms, malacostracans and polychaetes. There were insufficient data to examine gear and habitat effects on the other taxonomic groups (SI6 Appendix). For echinoderms (asteroids, echinoids, holothuroids, ophiuroids), it was only possible to examine the effect of OT, BT and TD. The "biogenic" habitat category was particularly poorly represented and could not be included in this model.

We used AIC to guide model selection. As is common practice in model selection using AIC values, models were ranked according to their AIC values such that the model with the lowest AIC was considered the "best/optimal" model (Burnham & Anderson, 2004). Models for which the difference in AIC relative to AIC_{best} was >2 were considered to have no support and fit the data poorly. Models for which the difference in AIC was <2 were considered to have substantial support, and we present the results for the model with the lowest AIC in the main text, and those for the model with Δ AIC <2 in the supplementary material. We have sought to apply this criterion consistently in all cases of model selection to avoid experimenter and methodological bias.

2.4.3 | Effects of other environmental variables

We also examined the effect of other variables that may influence depletion and recovery of benthic communities following fishing disturbance. To test for the effect of scale of disturbance, the minimum dimension of disturbed area (S_{min} in metres) was extracted from the source studies, as a proxy for the distances over which recolonization may occur. We explored the effects of S_{min} because rates of immigration of adults and larvae from nearby areas may be linked to the proximity of the impacted and control areas. To test for the influence of the history of fishing disturbance (FishHist) at the study sites, studies were divided into undisturbed and previously disturbed. Areas were defined as undisturbed, if they were known from fisheries-enforcement data to have been subjected to no or negligible fishing activity for at least 10 years prior to the fishing experiment, or were known to have remained unimpacted because they were in marine-protected areas or protected by seabed obstructions (Brown, Finney, & Hills, 2005; Pranovi, Raicevich, Libralato, Ponte, & Giovanardi, 2005). Areas were described as previously disturbed when subject to fishing disturbance in the last 10 years prior to the study (Castaldelli et al., 2003; Prantoni, Lana, Sandrini-Neto, Filho, & deOliveira, 2013). To test for any effects of environmental factors that influence the growth rates, and hence recovery rates, of individuals and populations, we considered primary production (PP, mg C m^{-2} day^{-1}) at each study site, as estimated from the vertically generalised productivity model (Behrenfeld & Falkowski, 1997); particulate organic carbon flux to depth (POC flux, g C_{org} m^{-2} $year^{-1}$, Lutz, Caldeira, Dunbar, & Behrenfeld, 2007); mean sea bottom temperature (SBT, °C) calculated from monthly mean bottom temperature for 2009–2011 all sourced from the MyOcean product "GLOBAL-REANALYSIS-PHYS-001-009"; mean water depth (Depth, m) from GEBCO if not reported in the original study, and "biogenic (%)," "gravel (%)," "sand (%)" and "mud (%)" as continuous variables extracted from source papers or from dbSEABED (http://instaar.colorado.edu/~jenkinsc/dbseabed/, Jenkins, 1997) when data were not provided in the articles. Different fishing gears have different levels of seabed contact and penetrate the seabed to different depths, and this physical modification of the seabed may also affect the rate of recovery following impact. The penetration depth (PD) for OT, BT, TD and HD into the seabed was estimated from values in the literature by averaging the reported penetration depths of the individual components of the gear (e.g. doors, sweeps and bridles of an OT) weighted by the width of these components (details in SI Text S2 of Hiddink et al., 2017). The mean PD for Dg and R studies was estimated from reported values in the examined studies included in this review. The average PD values used in the analysis are those reported in Table 1.

The full model examined was as follows: ln(RR) ~ $\log_2(t + 1)$ + FishHist + PD + S_{min} + depth + mud (%) + gravel (%) + SBT + POC. Since PP and POC, and sand (%) and mud (%), were strongly correlated (r = +.77, r = −.73, respectively), PP and sand (%) were dropped from the initial model to avoid collinearity of variables. POC was preferentially retained over PP because POC is a measurement at the seabed depth of the study, whereas PP is a water column attribute. Mud was chosen over sand as it correlates less than sand with gravel (Table SI7.5). Model selection was carried in the glmulti R package (Calcagno & de Mazancourt, 2010), which provides the necessary functionality for model selection and multimodel inference using an information-theoretic approach. The glmulti package examines the fit and plausibility of various models, focusing on models that contain none, one and up to all explanatory variables. Selection of the final model was based on values of the corrected Akaike's Information Criterion (AICc) and the plots of model-averaged importance of terms. The AIC_C was used here instead of the AIC because sample sizes were very small in relation to the potential number of model parameters.

3 | RESULTS

3.1 | Location and scope of studies

The majority of studies that passed the inclusion criteria were carried out in temperate waters of North Europe (43%), eastern North America (23%) and Southern Europe (14%) (Figure 1a). These are also the regions where most excluded studies were conducted. Most (89%) of the studies were undertaken at depths less than 40 m; of these 33 (30%) were in intertidal areas (Figure 1b). Otter trawling (22%) and towed dredges (27%) were the most frequently studied gear types (Figure 1c). Sand was by far the most commonly studied habitat and there were few studies on biogenic and gravel habitats (Figure 1d). Many gear-habitat combinations were not represented because many fishing gears are only suitable for fishing on particular types of seabed or species associated with those habitats and because some habitats are less widespread than others (SI6, Eigaard et al., 2016).

3.2 | Benthic community response and recovery

3.2.1 | Overall effect of bottom fishing

A pass of a bottom-contact gear (all gears and habitats combined) resulted in significant reduction in benthic community abundance

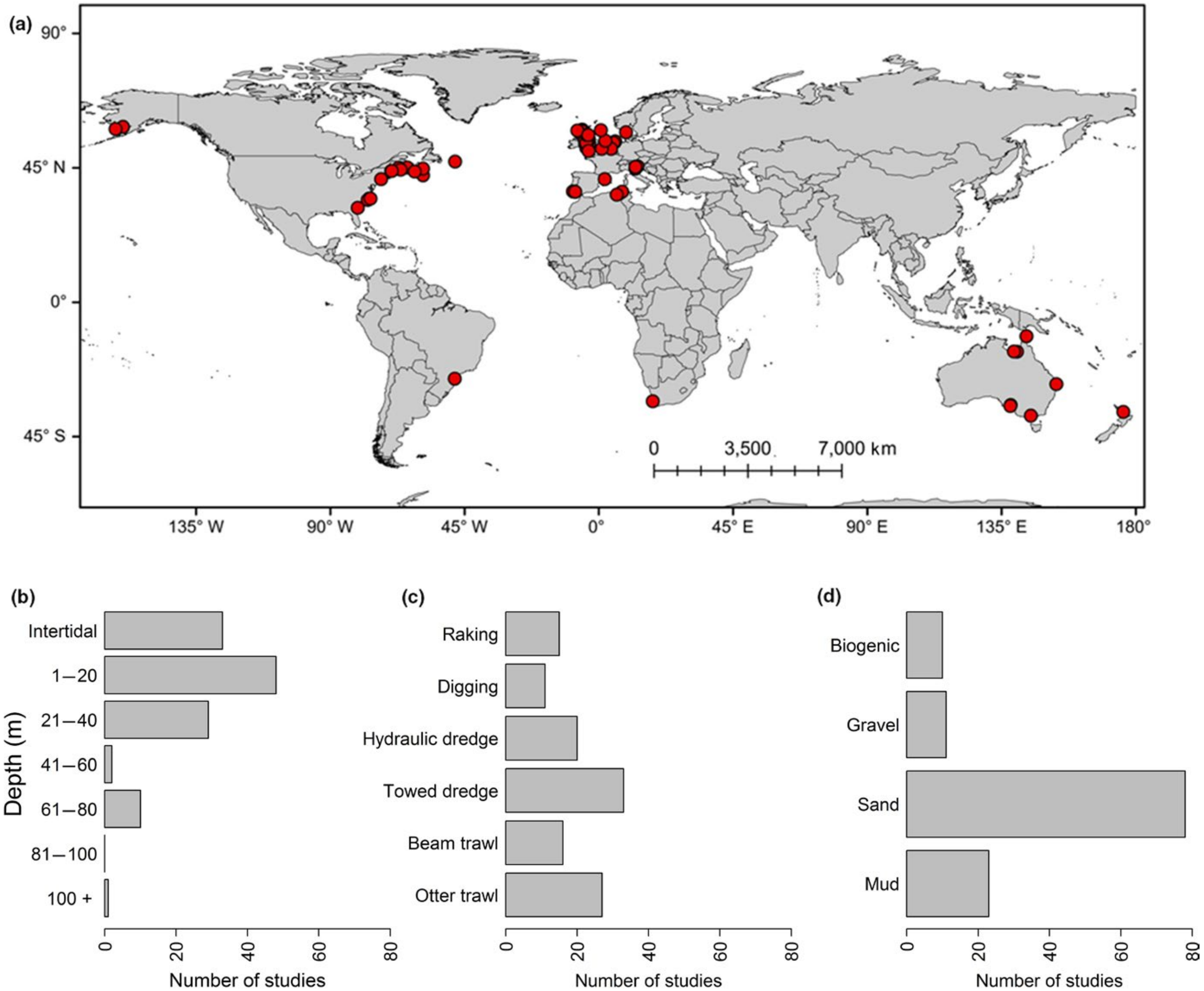

FIGURE 1 Summary of the distribution of published fishing impact studies with respect to (a) geographic location, (b) depth (m), (c) fishing gear used to create the fishing disturbance, (d) sediment type. 122 studies were identified from 62 publications [Colour figure can be viewed at wileyonlinelibrary.com]

(mean response, 95% CI: −20%, −27% to −12%) and number of species (−16%, −21% to −10%). When the effect of scavengers was removed, the reductions in community abundance were larger (−26%, −34% to −18%) and species richness (−19%, −25% to −13%). Benthic community abundance and species richness were predicted to take more than 3 years to recover following bottom fishing (SI7 Appendix, Table SI7.1). In the remainder of this paper, we only report results when scavengers are excluded because these provide unbiased estimates of depletion and recovery for the biota present at the time of the experiment, but the corresponding results with scavengers included are presented in the Supplementary Information, SI7.

3.2.2 | Effect of gear and habitat type

The initial response on benthic community abundance and species richness differed significantly among gear types (Figure 2a,c) but not among habitat types (Figure 2b,d). Reduction of community abundance was significantly higher for digging, raking and hydraulic dredging than for beam trawling, towed dredging and otter trawling (Q_M (*df* = 11) = 104.56, $p < .0001$, R^2 = 39.86%) (Figure 2a). Digging resulted in the largest reduction in community abundance (mean response, 95% CI: −70%, −77% to −61%), followed by raking (−53%, −66% to −37%) and hydraulic dredging (−32%, −48% to −11%). Towed dredges, beam trawls and otter trawls resulted in a mean initial response in community abundance of −8%, −12%, −3% per gear pass, and the response varied widely among studies for these gears (95% CI for mean response: TD = −20% to +5%, BT = −35% to +16%, OT = −32% to +38%). Digging and hydraulic dredging also resulted in significantly higher reductions in species richness than the other gear types (Q_M (*df* = 5) = 55.98, $p < .0001$, R^2 = 34.43%) (Figure 2c). The initial impact of digging and hydraulic dredging was to reduce community species richness by 32% (95% CI of mean response:

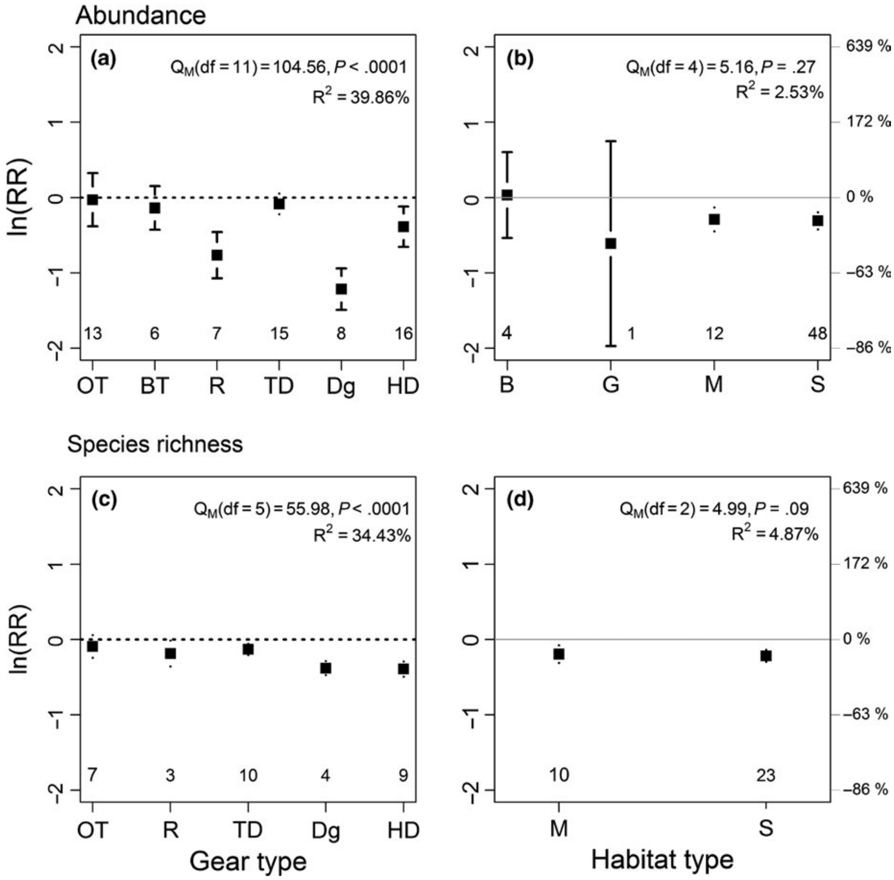

FIGURE 2 (a, c) Initial response (mean ln(RR) ±95% CI) of benthic community abundance and species richness to different fishing gears following a single gear pass (OT—otter trawling, BT—beam trawling, R—raking, TD—towed dredges, Dg—digging, HD—hydraulic dredges). (b, d) Initial response of benthic community to fishing in different habitat types (B—biogenic, G—gravel, S—sand, M—mud). It was not possible to examine effect of all gear and habitat types for species richness (see main text). The right-hand axis gives the % change for ease of interpretation. The Q_M statistic tests for differences among levels of the explanatory variables, gear type and habitat type. R^2 provides the amount of variability (in per cent) explained by the explanatory variable. The number of studies included in each estimate of depletion is given below each error bar. Data for studies with a scavenging effect are not presented (but see SM7, Table SM7.3)

Dg = −38% to −25%, HD = −39% to −25%), raking by 17% (−30% to −2%), towed dredges by 12% (−19% to −5%) and otter trawls by 9% (−22% to +6%) (Figure 2c).

The rate of recovery (slope) for benthic community abundance differed significantly among gear types (optimal model: gear + $\log_2(t + 1)$:gear), and was faster for Dg and R than for HD, BT, OT and TD (Figure 3). Nevertheless, time to recovery (t_c), which is a function of both initial response and recovery rate, was predicted to occur over shorter time scales for OT and BT than for other gear types because impact at $t = 0$ was variable and not significantly different from 0 for these gears (Figures 2a and 3). Recovery following Dg, TD and HD was predicted to take 3 years or longer (Figure 3). Time to recovery (t_c) for species richness depended on the gear type creating the disturbance (optimal model: gear + $\log_2(t + 1)$) and was longest for Dg and HD gear that resulted in the highest depletion in species richness upon impact (Figure 2c). Community species richness was predicted to recover within days following OT, within 1 and 4 months following TD and R, and to take more than 3 years following Dg and HD (Figure 4).

3.2.3 | Effect of environmental variables

Gear penetration depth, percentage mud content and the history of fishing disturbance of the study sites prior to experimental fishing were found to significantly influence the response of community abundance to fishing (Q_M $(df = 4) = 62.46$, $p < .0001$, $R^2 = 26.67\%$), resulting in a 3% and 0.3% further reduction in abundance for each centimetre of penetration depth and per cent of mud content, respectively (Table 2a). Community abundance was not predicted to recover to control conditions within 3 years when impacted by gears with penetration depth of ≥16 cm (Figure 5). Experimental fishing resulted in higher depletion in community abundance in undisturbed areas relative to previously disturbed areas, resulting in a further 12% reduction in abundance (Table 2a).

Gear penetration depth, percentage mud content, the presence of biogenic substrate and the history of fishing disturbance were found to significantly influence the effect of fishing on community species richness (Q_M $(df = 5) = 79.82$, $p < .0001$, $R^2 = 48.34\%$), with a further 2% and 0.1% reduction for each

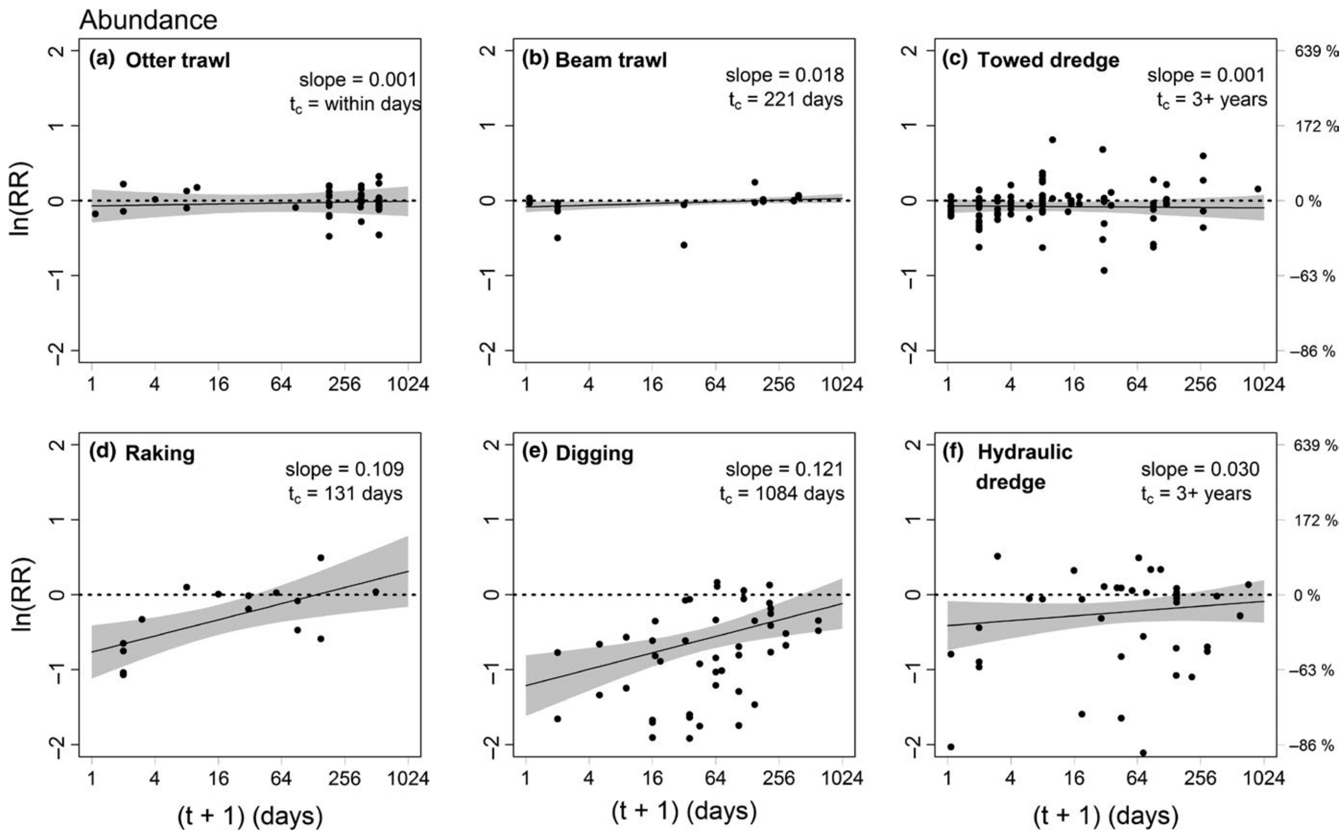

FIGURE 3 Recovery (solid lines) of benthic community abundance (with 95% confidence interval) following fishing with otter trawling (OT), beam trawling (BT), towed dredging (TD), raking (R), digging (Dg) and hydraulic dredge (HD). The slope (the rate of change in ln(RR) over time following the fishing disturbance event) and t_c (the predicted time required for abundance in the fished area to return to control conditions) are reported in the top right corner of each panel. The right-hand axis gives the % change for ease of interpretation. Black dots represent log response ratio data calculated for each study. Data for studies with a scavenging species effect are not presented (but see SM7, Table SM7.3)

centimetre of penetration depth and per cent of mud content, respectively (Table 2b). Community species richness was predicted to recover within months when impacted by gears with PD of 3 and 6 cm but to take longer than 3 years for gears with PD of 16 cm (Figure 6a–c). Conversely, recovery of species richness in biogenic habitats was not predicted to occur within 3 years for any of the gear penetration depths, indicating longer lasting effects of fishing in biogenic habitats no matter the gear PD (Figure 6d–f). Fishing resulted in a further 8% reduction in species richness in undisturbed areas relative to previously disturbed areas (Table 2b).

3.3 | Taxonomic group response and recovery

3.3.1 | Overall effect of bottom fishing

Initial response and recovery rates varied significantly among different taxonomic groups ($\log_2(t + 1) \times$ taxon: Class, $Q_M(df = 27) = 65.18$, $p < .0001$, $R^2 = 5.63\%$; Phylum, Q_M $(df = 19) = 41.76$, $p = .0019$, $R^2 = 3.14\%$). The largest significant reductions in abundance were observed for annelids of the class clitellata, mostly Oligochaeta (mean response, 95% CI: −55%, −74% to −22%), nematodes (−46%, −61% to −25%) and polychaetes (−31%, −39% to −20%) (Figure 7). Gastropods and bivalves also experienced a significant 31% (−41% to −18%) and 23% (−33% to −10%) reduction in abundance and appeared to be more sensitive to fishing disturbance than malacostracans (−16%, −26% to −5%) (Figure 7). Fishing also resulted in a significant reduction in ophiuroids abundance, −30%; however, the effect was highly variable within this taxonomic group (95% CI: −51% to −1%). When the effect of scavengers was removed, fishing resulted in a further 12% reduction for ophiuroids and 4% for asteroids (SI7 Appendix, Table SI7.8).

Gastropods, malacostracans (primarily decapods and amphipods, 74% and 19% of data, respectively), ophiuroids and polychaetes had the shortest recovery times to control conditions (t_c) of 1–1.5 months (Table 3). Bivalves and clitellates were predicted to return to control conditions within 4 and 7 months, respectively, following fishing (Table 3). Although the remaining taxonomic groups (bryozoans, ascidians, asteroids, poriferans, hydrozoans and holothuroids) tended to decrease in numbers and biomass following fishing, the initial response was highly variable and not statistically significant (Figure 7). This variation in response made it hard to predict recovery rates

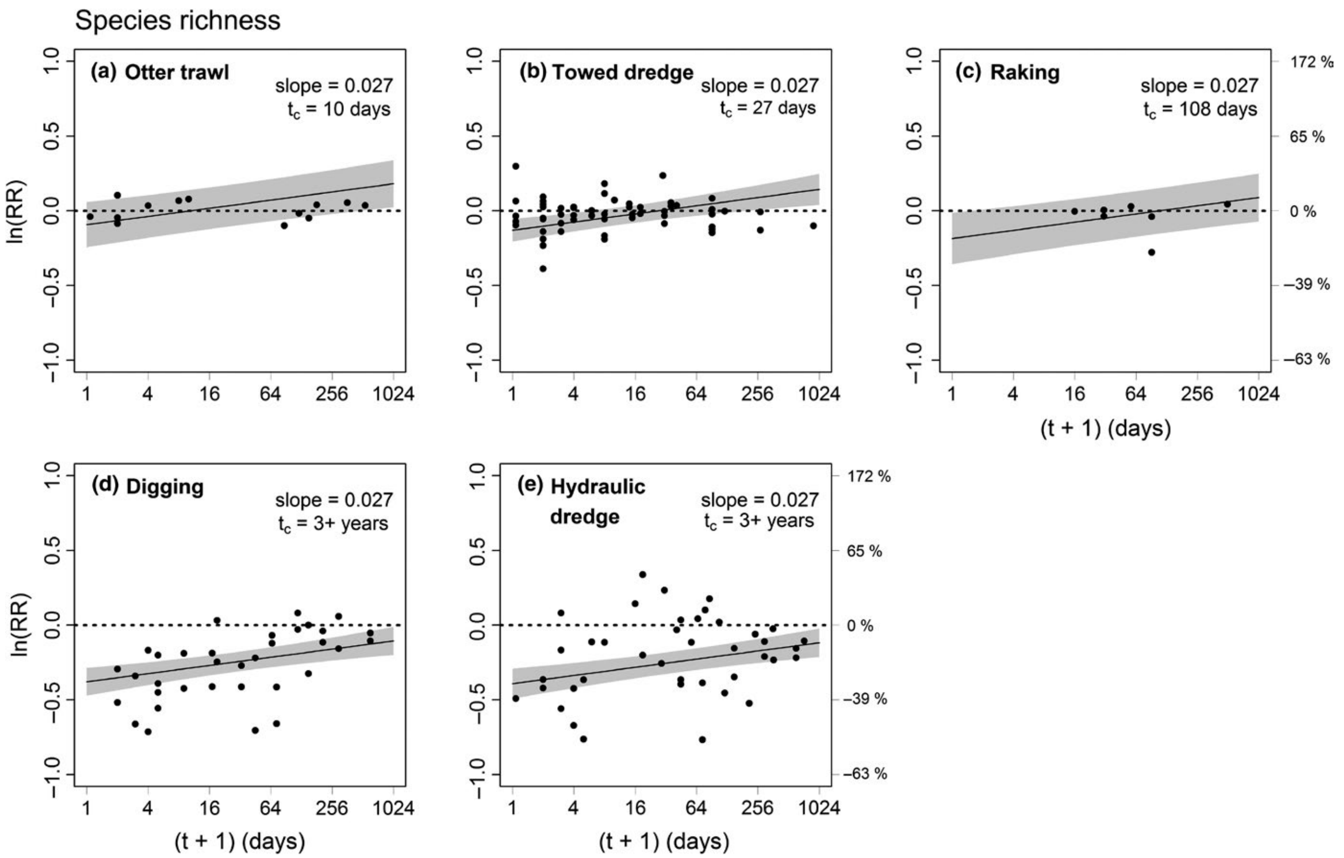

FIGURE 4 Recovery (solid lines) of benthic community species richness (with 95% confidence interval) following fishing with otter trawling (OT), towed dredging (TD), raking (R), digging (Dg) and hydraulic dredge (HD). The effect of beam trawling was not examined because there were insufficient data. The right-hand axis gives the % change for ease of interpretation. Black dots represent log response ratio data calculated for each study. Data for studies with a scavenging species effect are not presented (but see SM7, Table SM7.3)

(slope) and recovery times (t_c) accurately for these taxonomic groups (Table 3).

3.3.2 | Effect of gear and habitat type

The influence of gear and habitat type on the response of species abundance was taxon-specific. Depletion of bivalve, malacostracan and gastropod abundance differed significantly among fishing gears (Bivalvia: Q_M (*df* = 5) = 23.45, p = .0003, R^2 = 16.91%; Malacostraca: Q_M (*df* = 6) = 81.21, p < .0001, R^2 = 37.26%, Gastropoda: Q_M (*df* = 11) = 45.64, p < .0001, R^2 = 33.29%). Bivalves were depleted the most by hydraulic dredges (mean response, 95% CI: −39%, −50% to −28%) (Figure 8a). Malacostraca abundance was significantly reduced by digging (−58%, −66% to −47%) and by hydraulic dredges (−37%, −48% to −24%) (Figure 8b). Gastropods were most impacted by digging (−62%, −71% to −49%) and raking (−42%, −60% to −14%) (Figure 8c). Although OT, BT and TD tended to reduce the number of bivalves (range of mean response: −6% to −19%), gastropods (−1% to −24%) and malacostracans (−1% to −9%), the effects were highly variable and not statistically significant (Figure 8, SI7 Appendix Table SM7.10). The rate of recovery to control conditions for gastropods was also gear-specific; recovery was significantly faster after digging (Dg) and fishing with towed dredges (TD) and slowest for areas that had been raked (SI7 Appendix, Table SI7.10). Although digging generated the highest depletion in gastropod numbers (−62%), recovery was predicted to occur within 3 months of the disturbance, which is perhaps not surprising given the mobility of gastropods and the small-scale nature of hand-digging.

The response of polychaete abundance was habitat-specific; depletion was significantly higher in mud (mean response, 95% CI: −43%, −65% to −7%) than in sand (−26%, −42% to −5%) (Figure 8d). The initial response on gravel substrates was smaller than expected, perhaps because of the small number of replicate studies and high variability among studies. Whilst the effect of fishing was to reduce echinoderm abundance directly after fishing (mean response, 95% CI: −8%, −23% to +9%), the response did not differ significantly among gear or habitat types (Q_M (*df* = 1) = 0.72, p = .40, R^2 = 1%).

4 | DISCUSSION

Our meta-analysis of bottom fishing depletion and recovery is the most comprehensive to date. We not only provide updated estimates of parameters generated in previous syntheses (e.g. Collie

TABLE 2 Linear mixed-model fits for the analysis of data from experimental studies of fishing impacts on (a) benthic community abundance (numbers and biomass) and (b) species richness

Explanatory variable	Estimate	*SE*	LCI	UCI	z	*p*
(a) Benthic community abundance (numbers and biomass)						
$\log_2(t + 1)$	0.0381	0.0100	0.0186	0.0577	3.8211	.0001
PD (cm)	−0.0334	0.0052	−0.0437	−0.0232	−6.3870	<.0001
Mud (%)	−0.0029	0.0010	−0.0049	−0.0010	−2.9647	.003
Fishing history						
Undisturbed	−0.1081	0.0782	−0.2613	0.0451	−1.3831	.1666
Previously disturbed	0.0470	0.0730	−0.0962	0.1901	0.6431	.5202
Model: ln(RR) ~ 1 + FishHist + $\log_2(t + 1)$ + PD + MUD Q_M (df = 5) = 62.46, p < .0001, R^2 = 26.67%						
(b) Benthic community species richness						
$\log_2(t + 1)$	0.0364	0.0067	0.0234	0.0495	5.4724	<.0001
PD (cm)	−0.0239	0.0034	−0.0306	−0.0173	−7.0523	<.0001
Mud (%)	−0.0013	0.0006	−0.0025	−0.0002	−2.2328	.0256
Biogenic (%)	−0.0039	0.0014	−0.0067	−0.0012	−2.7719	.0056
Fishing history						
Undisturbed	−0.0539	0.0524	−0.1566	0.0488	−1.0283	.3038
Previously disturbed	0.0465	0.0492	−0.0496	0.1426	0.9480	.3431
Model: ln(RR) ~ 1 + FishHist + $\log_2(t + 1)$ + PD + MUD + Biogenic Q_M (df = 5) = 79.82, p < .0001, R^2 = 48.34%						

For community abundance, the model with the lowest AIC included time since disturbance event ($\log_2(t + 1)$), gear penetration depth (PD), percentage mud content of the sediment (Mud %) and fishing history (FishHist). For community species richness, the model with the lowest AIC included $\log_2(t + 1)$, PD, percentage mud and biogenic content of the sediment (Mud %, Biogenic %) and FishHist. Estimate values give the change in response variable per unit increase in explanatory variable. *SE*, LCI and UCI indicate standard error, lower and upper 95% confidence interval, respectively. The Q_M and R^2 statistics for the optimal model are provided.

et al., 2000; Kaiser et al., 2006), but also significantly extend the coverage of gear and habitat types and consideration of the effects of environmental variables on depletion and recovery. The meta-analysis of Kaiser et al. (2006) considered literature until 2002, here; we include more recent literature of gear impact experiments to 2014. This literature has grown in response to societal concerns about the environmental effects of fishing and the need for quantitative evidence on the scale and magnitude of fishing effects. In contrast to previous syntheses, we only include experimental fishing studies and exclude comparative studies (analyses of impacts based on gradients of fishing effort in real fisheries, examined by Hiddink et al. (2017)) because the former provide the most reliable estimates of the timing and frequency of gear passes, as required to estimate initial response. We applied rigorous study quality assurance and excluded studies if they lacked the variability data required to weight studies and to quantify uncertainty around mean estimates of depletion and recovery reliably. Other advances in the present meta-analysis include the specific consideration of the effects of scavengers, which our results showed to be large and to bias estimates of depletion and recovery. The inclusion of scavengers reduced the apparent impact of fishing on community abundance and species richness, and also on taxonomic groups which include scavengers, such as ophiuroids, asteroids and malacostracans. In contrast to previous analyses of experimental data, we adjusted ln(RR) for the number of gear passes (f). Results are therefore standardized per gear pass, as is required for predictions of the effect of different fishing intensities, and this is one reason why our estimates of depletion are generally lower than those in Collie et al. (2000) and Kaiser et al. (2006).

Our analyses have shown that the depletion in abundance and species richness is highly variable and depends on gear and sediment types, the taxa considered and the history of fishing at the experimental site. Depletion was greater when experiments were conducted on previously unfished experimental sites, and higher for taxonomic groups with no or limited mobility (e.g. ascidians, polychaetes, bivalves) or surface dwellers (e.g. bryozoans, sponges, gastropods). Both gear type and the penetration depth of the gear into the sediment had a significant influence on depletion. The depletion caused by raking (R) and digging (Dg) and gears such as hydraulic dredges (HD) was more severe than that of otter (OT) and beam trawling (BT), and likely related to the increased physical disturbance resulting from deeper penetration into the sediment. Although the overall effect of OT, BT and towed dredges (TD) was to reduce community abundance (range of mean response: −3% to −12%) and species richness (range: −9% to −12%), the effect was not significant given high variance. Nevertheless, given that our estimates are based on all available evidence to the date of this review, it seems

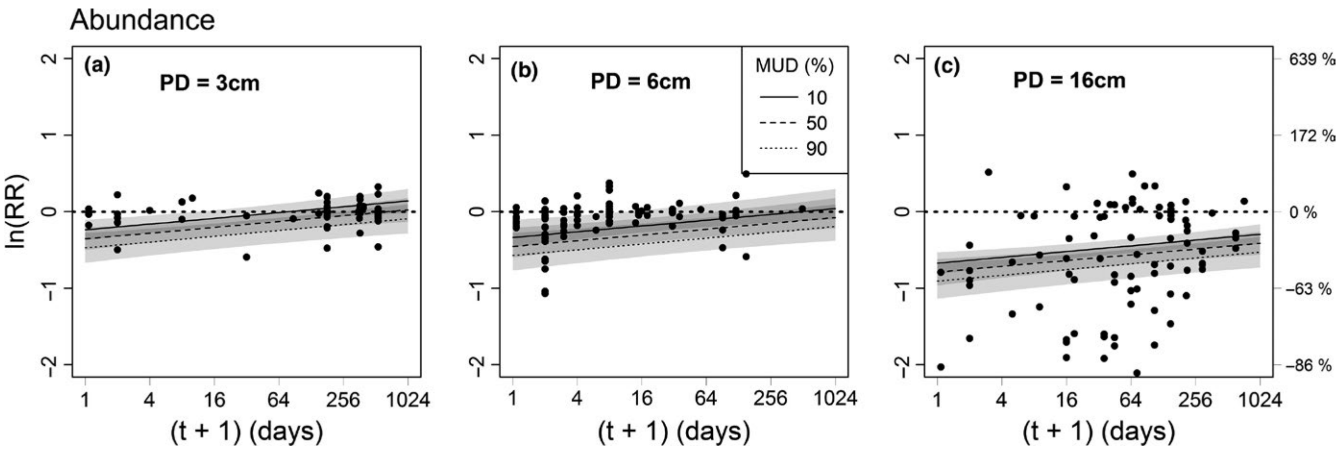

FIGURE 5 Post-fishing recovery trends of benthic community at different gear penetration depth (PD, where 3 cm is typical of OT and BT, 6 cm is typical of TD and R, 16 cm is typical of Dg, HD) in sediment with 10%, 50% and 90% mud content that had been undisturbed by fishing for the last 10 years. Shaded areas indicate the 95% confidence interval for the estimated fit. The right-hand axis gives the % change for ease of interpretation

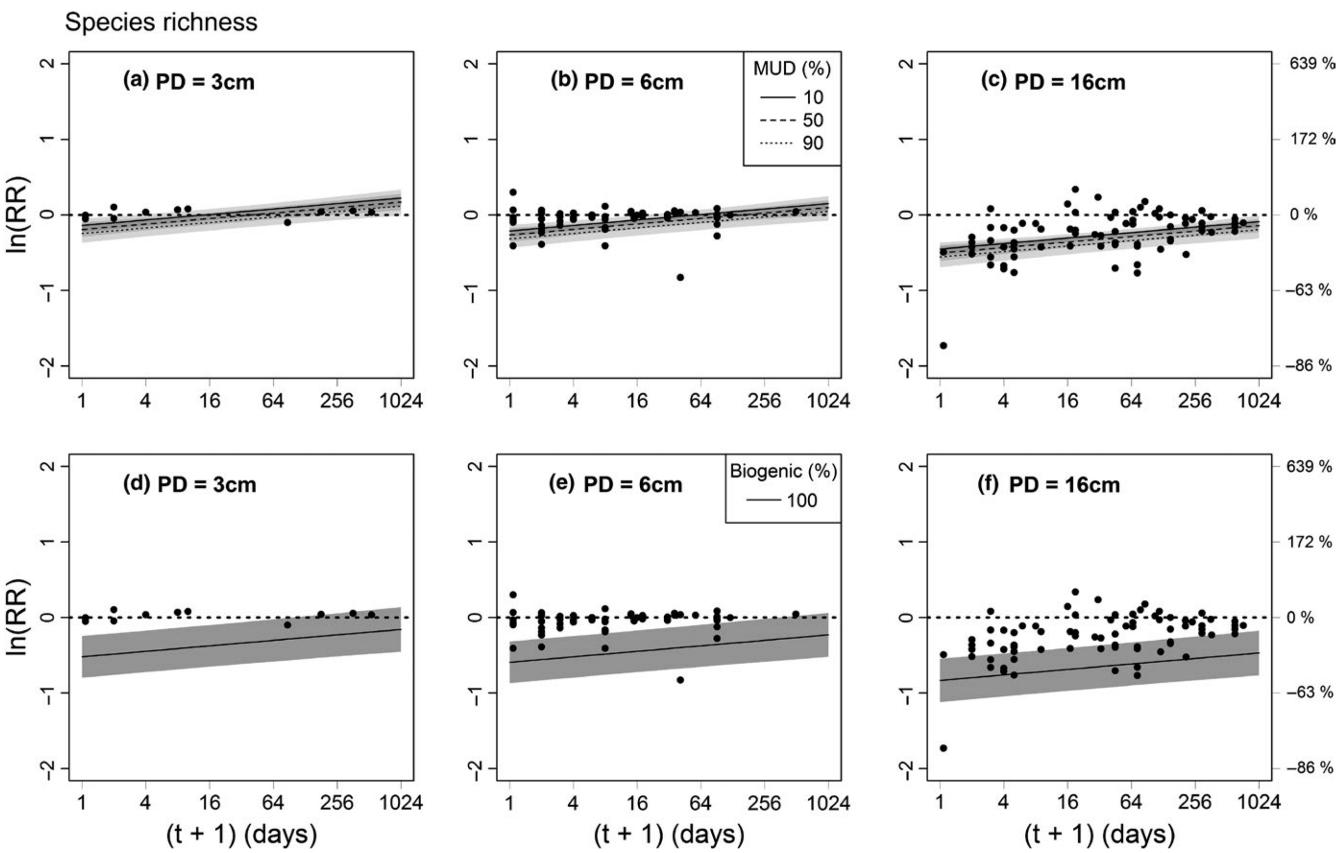

FIGURE 6 Post-fishing recovery trends of benthic community species richness at different gear penetration depth (PD, where 3 cm is typical of OT and BT, 6 cm is typical of TD and R, 16 cm is typical of Dg, HD) in (a–c) sediment with 10%, 50% and 90% mud content and (d–f) in biogenic habitats. Shaded areas indicate the 95% confidence interval for the estimated fit. The right-hand axis gives the % change for ease of interpretation

reasonable to assume that these estimates are close to the real mean values of depletion caused by these towed gears and practitioners should use these estimates in assessments (rather than assume that depletion is zero as a strict hypothesis testing framework would dictate).

While some of the variability around the mean estimates of community depletion was attributed to the gear type, penetration depth, habitat and taxonomic effects, much of the between-study variation remained unexplained. Sources of variation that could not be addressed with data available in the studies included differential

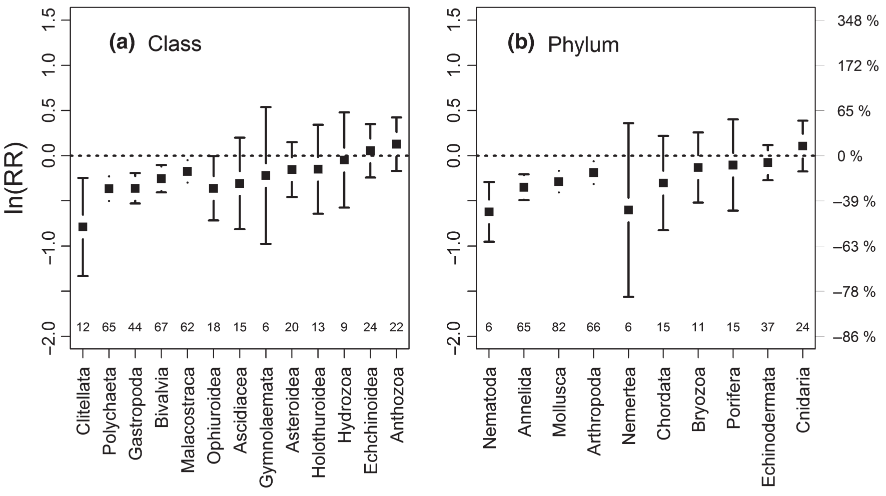

FIGURE 7 Initial response (mean ln(RR) ±95% CI) to fishing of taxon abundance per gear pass. The horizontal dotted line at ln(RR) = 0 represents equal abundance in fished and control areas. If the 95% CI overlaps ln(RR) = 0, the effect of fishing is not significant. The right-hand axis gives the % change for ease of interpretation. The number of studies included in each estimate of depletion is given below each error bar. Data for studies with a scavenging effect are not presented (but see SM7, Table SM7.8)

TABLE 3 Post-fishing recovery rate (slope) and recovery time (t_c) for different taxonomic groups

	Slope	*SE*	LCI	UCI	z	*p*	t_c (days)
Taxon abundance							
Nematoda	0.0369	0.0367	−0.035	0.1088	1.0051	.3148	1,095+
Clitellata	0.1015	0.0529	−0.0021	0.2052	1.9194	.0549	218
Bivalvia	0.0367	0.0287	−0.0197	0.093	1.275	.2023	123
Polychaeta	0.0675	0.0285	0.0115	0.1234	2.3644	.0181	42
Malacostraca	0.0343	0.0278	−0.0202	0.0888	1.233	.2176	33
Gymnolaemata	0.0438	0.056	−0.066	0.1535	0.7813	.4346	31
Ophiuroidea	0.0747	0.0377	0.0008	0.1486	1.9804	.0477	28
Gastropoda	0.0781	0.0293	0.0207	0.1355	2.6672	.0076	24
Nemertea	0.174	0.1504	−0.1207	0.4687	1.1573	.2472	10
Ascidiacea	0.1003	0.0508	0.0007	0.1998	1.9745	.0483	7
Asteroidea	0.0604	0.0369	−0.0118	0.1327	1.6397	.1011	5
Hydrozoa	0.0246	0.0496	−0.0726	0.1218	0.4966	.6195	3
Holothuroidea	0.1233	0.0597	0.0062	0.2403	2.0642	.039	2
Echinoidea	0.0555	0.0364	−0.0158	0.1268	1.5267	.1268	NA
Anthozoa	−0.0348	0.0251	−0.0841	0.0144	−1.3854	.1659	NA
Bryozoa	−0.0203	0.0307	−0.0804	0.0398	−0.6633	.5071	NA
Porifera	−0.0067	0.0414	−0.0878	0.0745	−0.1611	.872	NA

SE, LCI and UCI indicate standard error, lower and upper 95% confidence interval, respectively. Data for scavenging species within the first 2 days following the fishing disturbance have been removed from the analysis. NA indicates not applicable (i.e. when intercept is a positive value or slope a negative value).

responses of species within communities or taxa, which depend on what species were present in the study area. These are expected to be driven by differences in life histories (e.g. growth rates, age at maturity, longevity), morphology (e.g. shape, structures) and ecological attributes (e.g. mobility, position on/within the sediment). A large proportion of less sensitive species in any given grouping (community, taxon) may mask the response of more sensitive but less abundant species. Given that the majority of studies included in the meta-analysis were carried out at depths <40 m (OT = 59%, BT = 83%, TD = 100% of studies) and in sand (OT = 65%, BT = 83%, TD = 94% of studies), where levels of natural disturbance from waves and tidal currents are expected to be high, many of the environments studied will favour smaller species with faster life histories that are more resilient to fishing. Indeed, both experimental and comparative studies reported smaller effects of fishing in high-energy environments and dynamic habitats (Bergman & van Santbrink, 2000; van Denderen, Hintzen, Rijnsdorp, Ruardij, & van Kooten, 2014; van Denderen et al., 2015; Hall-Spencer & Moore, 2000; Kaiser et al., 1998).

Depletion estimates are essential input parameters to quantitative models of the fishery-scale effects of bottom fishing (Duplisea, Jennings, Warr, & Dinmore, 2002; Ellis, Pantus, & Pitcher, 2014;

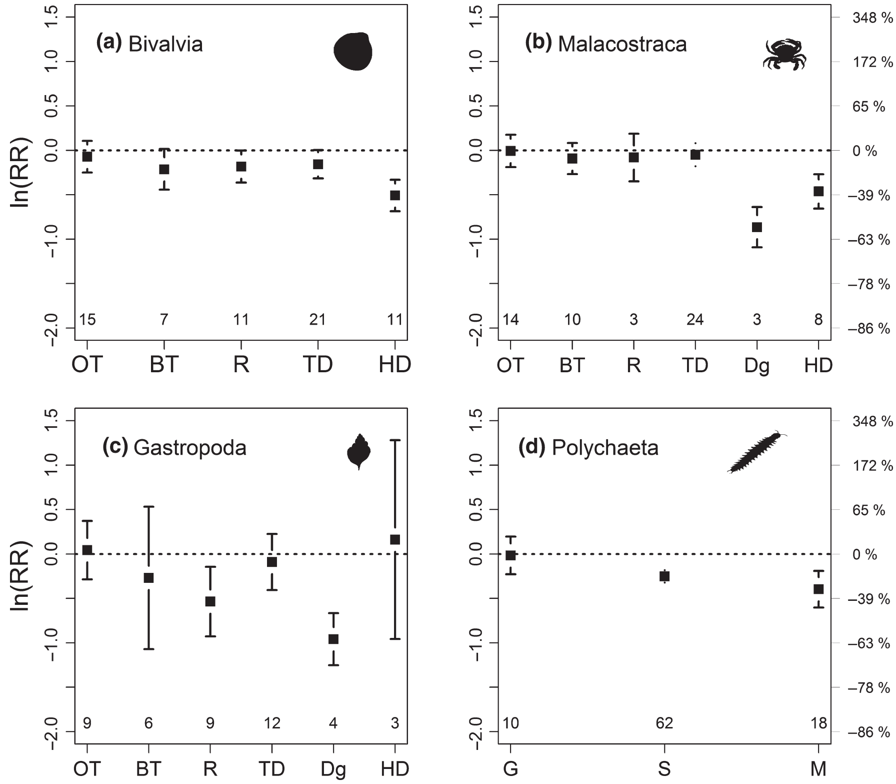

FIGURE 8 (a–c) Initial response (mean ln(RR) ±95% CI) of bivalve, malacostracan and gastropod abundance to otter trawling (OT), beam trawling (BT), raking (R), towed dredging (TD), digging (Dg) and hydraulic dredging (HD). (d) Initial response of polychaetes to fishing in gravel (G), sand (S) and mud (M). The effect of Dg on bivalves and of biogenic habitat on polychaetes is not presented due to insufficient sample size. The horizontal dotted line at ln(RR) = 0 represents equal abundance in fished and control areas. If the 95% CI overlaps ln(RR) = 0, the effect of fishing is not significant. The right-hand axis gives the % change for ease of interpretation. The number of studies included in each estimate of depletion is given below each error bar. Data for scavenging species were removed

Hiddink, Jennings, & Kaiser, 2007; Pitcher et al., 2016a) and our meta-analyses provide parameter estimates, and associated uncertainty, for use in future modelling exercises. Since initial response estimates are presented on a "per pass" basis, they can be used to estimate total depletion at any given frequency of fishing. Our reported gear effects can be linked to differences in the penetration depth of the gear because different categories of gears have characteristic penetration depths (Eigaard et al., 2016; Hiddink et al., 2017). When penetration depth can be estimated for a given gear, we propose that penetration depth is used directly to estimate depletion using the statistical relationships presented here. This approach can be applied to many and evolving gear configurations and can estimate differences in depletion resulting from differences in penetration depth of gears that would otherwise be assigned to a single gear category. When details of a gear are insufficiently specified to estimate penetration depth, then gear type can be used to predict depletion, albeit with increased uncertainty. Since experimental depletion estimates also depend on the inclusion of scavengers and the previous history of fishing at the experimental site, we recommend using estimates of depletion that exclude scavengers and exclude experiments conducted in previously fished areas. Inclusion would result in an underestimation of the impact on the benthos as we found higher reductions in community abundance and slower recovery times for areas that were unfished prior to experimental fishing relative to those that were regularly fished. This is likely to result from shifts in community composition towards species with faster life histories that are resilient to further fishing in regularly fished areas (e.g. Hiddink et al., 2017; Jennings, Greenstreet, & Reynolds 1999). Taxon-specific estimates for depletion would be used when modelling fishery-scale impacts on specific taxa. The recommended treatment of links between penetration depth, gear type and depletion relate to fishing on sediments, since no experiments included in the meta-analyses were conducted on hard ground (e.g. bottom trawling over rock).

Our analyses show that recovery rates depend not only on the magnitude of depletion following the passage of the gear, but also on habitat type and taxon. Community recovery to control conditions was slower for communities fished by gears that penetrated deeper in the sediment and killed a larger fraction of biota (Dg, R, HD, TD) than for gears that penetrated less (BT, OT). It is worth noting, however, that while BT and OT have the least impact per unit area of seabed compared to Dg, R and HD, the spatial scales at which BT and OT are operated in commercial fisheries are magnitudes higher than those for the other gear types. In Table 1, we provide data on the area disturbed per experimental plot by each gear type in the studies examined to understand better the commercial importance and breadth of impact for each gear (e.g. Dg: 4 m^2 vs. OT: 120,000 m^2). Therefore, whereas depletion and time to recovery may appear to be small and short for OT and BT, the scale of areas disturbed by these fisheries may result in slower recovery times than those suggested by these experimental studies. Furthermore, recovery times (t_c) were faster in areas that were fished prior to experimental fishing. A recent meta-analysis of recovery rates, based on large-scale comparative studies across effort gradients on commercial fishing grounds (Hiddink et al., 2017), also demonstrated faster community recovery rates in areas with higher levels of trawling. We consider both these results to be a consequence of shifts in community composition towards species with faster life histories in fished areas (e.g. Jennings, Dinmore, Duplisea, Warr, & Lancaster, 2001; Jennings, Freeman, Parker, Duplisea, & Dinmore, 2005), since recovery of community-wide abundance is then driven by the dominance of the species with fast life histories. For this reason, the recovery of community-wide abundance is not equivalent to the recovery of community life-history structure which would be much slower and involve an increase in the relative abundance of species with slow life histories.

Despite the large impacts of fishing on their abundance, polychaetes recovered within a few months of the disturbance event, which is not surprising given that the majority of studies (75%) were for free-living polychaete species with high intrinsic rates of growth, allowing them to colonize quickly and to recover rapidly from disturbance (Asch & Collie, 2005; Jennings, Pinnegar, Polunin, & Warr, 2002). Malacostracans that were primarily comprised of mobile genera such as *Crangon*, *Carcinus*, *Corystes* and *Pagurus* also recovered quickly from fishing disturbance, presumably because they can recolonize impacted areas more quickly than sessile or low mobility species groups. Conversely, bivalves and sessile taxa such as ascidians and bryozoans showed little or no short-term recovery (within the 3-year time frame of the studies examined). For these species, recovery largely depends on recruitment, settlement and growth in impacted areas and the extent of substrate modification following the fishing event. For example, many sessile invertebrates such as anemones, tunicates and soft corals in sandy disturbed areas of the Bering Sea depend on empty shells for attachment, and trawling can bury these shells and hamper their recovery (McConnaughey & Syrjala, 2014).

Our estimates of recovery times from fishing experiments were generally shorter than estimates from the large-scale comparative studies of Hiddink et al. (2017). Although direct like for like comparisons are not feasible because their study only estimated the time for abundance to recover to between 50% and 95% of the theoretical unfished abundance assuming logistic population growth, we attribute this difference to the much smaller areas of seabed disturbed during fishing experiments, and thereby the much larger importance of active and passive movement of biota and recolonization or recruitment. These processes support potentially faster recovery when the impacted area is nearer to an unfished or infrequently fished area, since the observed recovery is less dependent on the reproduction and growth of organisms remaining in the impacted area. Real fishing grounds are generally composed of a mosaic of unfished, recently fished and recovering benthic communities and habitats and within grounds recovery of fished areas is slower when they are more isolated from unfished areas (Lambert, Jennings, Kaiser, Davies, & Hiddink, 2014). Therefore, while our comparisons of recovery rates from meta-analyses of experimental (this paper) and comparative (Hiddink et al., 2017) studies are informative in relation to understanding how the spatial scale of fishing disturbance will affect recovery, we recommend that the recovery estimates from comparative studies are used for analyses at the fishery scale whenever they are available for the community or relevant taxonomic groups. However, recovery estimates from experimental studies may be chosen preferentially in studies of recovery following isolated and perhaps unauthorised fishing impacts in areas otherwise closed to fishing and in studies of small fisheries with very small fishing footprints.

Despite the proliferation of fishing impact experiments in recent years, the screening of studies for our meta-analysis revealed some key information gaps in the scope, conduct and reporting of studies. First, there are very few studies in the tropics or polar regions and several potential gear and habitat combinations that have not been studied. The absence of gear and habitat combinations is partly attributed to the links between fishers' gear choice and habitat type (Eigaard et al., 2017). However, this means that we lack estimates of depletion and recovery time for gear and habitat combinations that matter to society and managers, including the effects of trawling on hard ground (rock) and the effects of a range of gears on biogenic habitats. The non-significant results for gravel in this study are likely due to the low numbers of experiments conducted on this substrate. The relatively fast recovery times for community species richness impacted by towed dredge gear (1 month) is likely due to the fact that 77% of the studies examined were carried out on sand (where communities have been shown to recover faster) and due to the short duration of the experiments analysed (only 22% of the data was measured between 1.5 and 30 months following the disturbance). Second, most studies report experimental fishing impacts on aggregate abundance or the abundance of broad taxonomic groups. While this may adequately describe fishing impacts when grouped fauna show similar responses to fishing, they are more likely to respond differentially depending on morphology, body size and distribution in sediment. More highly resolved reporting of species' responses would allow more flexibility when grouping fauna in the meta-analyses and consequently to describe impacts on defined groups of relevance to society or managers. Although response in terms of species richness provides useful management information, it is worth pointing out that we may have overestimated the decrease in species richness attributed to fishing due to the fact that fewer species are sampled because numerical abundance is lower in impacted areas. Rarefaction curves of number of species as a function of number of samples or as a function of the accumulated number of individuals per sample would generate more accurate species richness estimates among impacted and control areas. However, these could not be calculated as count data of the number of species found in each sample collected from the impacted and control area was not readily available from source papers of bottom fishing experiments.

The Ecosystem Approach to Fisheries Management requires managers to consider the environmental impacts of fishing in management plans (Pikitch et al., 2004; Rice, 2014) and many other groups in society including Non-Governmental and Inter-Governmental Organizations and certification bodies seek assessments of fishing impacts. Our meta-analysis provides estimates of the gear, habitat and taxon-specific depletion of biota as an immediate consequence of a fishing event. It also provides insights into the dynamics of recovery and, considered alongside other studies, demonstrates the influence of the spatial scale of impact on recovery rates. Specifically, our estimates of depletion along with estimates of recovery rates (Hiddink et al., 2017) and large-scale, high-resolution maps of fishing frequency and habitat (e.g. Eigaard et al., 2017) will enable further analysis of bottom fishing impacts on regional scales (e.g. Mazor et al., 2017; Pitcher et al., 2016a; Rijnsdorp et al., 2016).

ACKNOWLEDGEMENTS

We thank Chris Jenkins for providing dbSEABED data. The study was funded by David and Lucile Packard Foundation, the Walton Family Foundation, The Alaska Seafood Cooperative, American Seafoods Group US, Blumar Seafoods Denmark, Clearwater Seafoods, Espersen Group, Glacier Fish Company LLC US, Gortons Inc., Independent Fisheries Limited N.Z., Nippon Suisan (USA), Inc., Pacific Andes International Holdings, Ltd., Pesca Chile, S.A., San Arawa, S.A., Sanford Ltd. N.Z., Sealord Group Ltd. N.Z., South African Trawling Association and Trident Seafoods. Additional funding to individual authors was provided by the UK Department of Environment, Food and Rural Affairs (project MF1225); Natural Environment Research Council and Department for Environment, Food and Rural Affairs (grant number NE/L003279/1); Marine Ecosystems Research Programme; the European Union (project BENTHIS EU-FP7 312088), the US National Oceanic and Atmospheric Administration (RAM). The International Council for the Exploration of the Sea (ICES) Science Fund, the Food and Agriculture Organisation of the UN.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Sciberras M, Hiddink JG, Jennings S, et al. Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish Fish*. 2018;19:698–715. https://doi.org/10.1111/faf.12283